

THE REPRODUCTIVE STRUCTURES OF
PLEURICOSPORA

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The genus *Pleuricospora*, with the single species *P. fimbriolata*, was described by Gray (7) as collected by Bolander "in or near the Mariposa *Sequoia gigantea* Grove" (Mariposa County, California). It is a saprophytic plant of the monotropoid alliance, not uncommon in the Sierra Nevada; but as it is less conspicuous than its allies *Sarcodes* and *Pterospora*, it is less familiar. It occurs also in the Coast Range of California and in Oregon and Washington. Two species have been described in addition to the one usually recognized. Of *P. longipetala* Howell, from Oregon, I have seen no material. As to *P. densa* Small (16), from the Sierra Nevada, neither the description nor a fragment of the type in the herbarium of the University of California shows any character by which it would be distinguished in the presence of a good range of specimens of *P. fimbriolata*. All herbarium specimens of *Pleuricospora* seem to have been collected during the months June to August inclusive.

I have been led to the study of pyroloid and monotropoid plants by a number of factors, one of which is the beauty and abundance of several species at Jonesville, in the Sierra Nevada in Butte County, California, at an altitude of about 5000 feet. It is by chance rather than for any definite reason that I am now ready to describe *Pleuricospora* rather than one of the others. I have seen it in the forests summer after summer, and have prepared microtome sections representing a considerable range of stages. Ordinary microtechnical methods were used; as a fixative, usually Bouin's fluid; as stains, Heidenhain's haematoxylin, Delafield's haematoxylin and safranin, safranin and light green, acetocarmine and aniline blue. The development of pollen was studied in plants dug up in the mountains and brought to Sacramento in the valley, where they developed rapidly; Belling's (3) iron-acetocarmine technique was applied, and impressed me by its usefulness. I cannot as yet elucidate some of the most interesting features of the plant; I have not worked out the detailed anatomy of stem and root; and experimental work will be necessary before one can say anything of the mycorrhiza with which the roots are clothed, of its relation to the life of the plant, or of the germination of the seeds.

It is a pleasure to acknowledge the many obligations which I have contracted in pursuing these studies. I am indebted to my father, Dr. E. B. Copeland, who made the observation of pollination noted below; to my colleagues, Dr. H. J. Child, Mr. George Kimber, and Miss Mary Cravens; and to our students, Mr. Frank

Dutra, who identified the bee, *Bremus vosnesenskii*, and especially Mr. Taiichi Asami, who prepared the slides from which several of the drawings were made.

GENERAL STRUCTURE

The plant is found chiefly in forests of silver-tip fir (*Abies concolor* Lindl. and Gord.) in ground covered by masses of decaying needles. As seen, it consists of little subglobular inflorescences projecting two or three centimeters above the surface (text fig. 1). They are white in bud or young flower, later turn-



Fig. 1. *Pleuricospora fimbriolata* Gray. Fruiting plants *in situ* $\times 1/2$. Photograph by F. S. van Eckhardt.

ing yellow, brown, or black. By digging, one finds that the inflorescences stand on peduncles several centimeters long, which arise from masses of slender roots. The roots are usually located in the soil beneath the decaying fir needles; their branching is, in part at least, exogenous; but the shoots arise endogenously. In July or August, young shoots, from a millimeter or so to several centimeters long, are to be found among the ones already in flower (pl. I, fig. 1); microscopic examination of the longer ones shows flowers with the parts already differentiated. If one marks the location of a cluster and digs early the next June (this is not summer, but early spring in the mountains), one finds them somewhat more highly developed; the anthers contain pollen mother cells. The sap of the shoots is sweet, and gives a strong positive reaction with Fehling's solution. In late June and along through July, when pollen is fully formed but before the ovules are ready for fertilization, the shoots appear above ground. The flowers open in acropetal order, but the uppermost ones often remain closed. Maturing and mature fruits are found in late July and in August.

The shoots are clad with scales, of which the lower may be called "leaves" on the "peduncle," and the upper "bracts" on the "rachis." They are all essentially alike, ovate to lanceolate, sharp pointed, more or less lacerate. The phyllotaxy is irregular and variable. Sometimes one finds a spiral, but not a typical spiral referable to the orthodox $1/2$, $1/3$, $2/5$, etc., system; more

often the scales are in whorls; on most shoots the number of members in the whorl is constant, and is either four, five, or six (pl. I, figs. 1, 2).

The flowers are solitary in the axils of the bracts, and are, of course, whorled as the bracts are (pl. I, fig. 2). In bud, the flowers are strictly sessile; but a pedicel grows as flower and fruit develop, and may reach a length of five millimeters. The cluster is, then, a spike or raceme; the lower pedicels show no tendency to bear lateral flowers, as in *Hypopitys*, *Newberrya*, and *Pityopus*.

The flowers (pl. I, figs. 3-14) are hypogynous and choripetalous, and with rare exceptions the parts are tetramerous. All parts are glabrous. Of sepals, one lies against the axis, that is, in a ventral position, and one against the bract, that is, in a dorsal position; these two are flattened; the other two, the lateral ones, are keeled. Sepals reach a length of 5 to 10 mm. The petals, placed alternately to the sepals, so that two of them may be regarded as ventral and two as dorsal, reach a slightly greater length. Sepals and petals, like the scales, are more or less lacerate. Details of the floral diagram—matters of the overlapping of one sepal or petal by another—vary from flower to flower. A stamen lies opposite each perianth segment. The anthers reach a length of three or four millimeters, and contain distinct pollen grains, before the filament begins to develop. As the flower approaches anthesis and finally reaches it, by the elongation of sepals, petals, and pistil, the anther grows but little; the filament grows to its full length, longer than the anther, in the course of a week or so, carrying the summit of the anther to about the level of the tips of the sepals. The flask-shaped pistil, about as long as the sepals and stamens, bears at the base a whorl of eight inconspicuous blunt nectaries, which, in the mature flower, project between the bases of the filaments. The style is short, not definitely marked off from the ovary; the stigma is narrow, its upper surface divided into four lobes. The style is traversed by an open channel, cruciform in cross section, and leading into the cavity of the ovary. The ovary contains (in almost all flowers) four placentae; these are densely covered with small ovules. The lobes of the stigma, and the placentae, are opposite the sepals. These structures mark the boundaries of the theoretical carpels, of which there are, therefore, four, opposite the petals.

The opening of the corolla is at first merely by a separation of the tips of the petals, affording but a narrow passage down to the viscid stigma (pl. I, figs. 12, 13). The flower remains in this state for two or three days. At this stage, it is found to have a faint, but definite, orchid-like odor; and nectar can be found about the base of the pistil. The anthers have developed in lateral contact with each other, and are now found to form a cylinder about the style, not projecting above the stigma. Dehiscence is approximately contemporaneous with the opening of

the corolla. Two lengthwise ribs are formed in each anther, by the contraction of a somewhat thick-walled, but not ribbed, exothecium. In fresh material, and in material preserved in liquid, the valves are not seen to gape widely; they separate to a distance about equal to the thickness of the anther, so that the spaces between each anther and the adjacent ones become filled with loose pollen grains. My microtome sections (pl. II, fig. 3) are of course made from completely dehydrated mature material, and show the valves completely straightened out.

It is evident that pollination is by insects; presumably by minute insects, or insects with a slender proboscis at least a centimeter long, to reach between the anthers to the base of the filaments and pick up the pollen on the way. Only one definite observation of a visit of an insect has been made; this was by a bee which has been identified as *Bremus vosnesenskii* (Radoszkowski). This is the common bee of the Sierra Nevada which is recognized by a large white patch on the back; it has been seen visiting other flowers of the neighborhood, both white and colored, as *Carum Gairdneri*, *Veratrum album*, and *Sidalcea spicata*.

After a few days, the flower opens more widely. This is accomplished chiefly by a movement of the two dorsal or abaxial petals; the two petals against the rachis remain erect. The flower is, it appears, definitely but obscurely zygomorphic (pl. I, fig. 14). The anthers are free to fall out of their compactly cylindrical arrangement, and may project above the stigma. Pollination is probably accomplished, under normal conditions, before this opening occurs; the complete opening of the flower seems merely to be the first stage of its withering.

The fruit (pl. V, figs. 1, 2) on its gradually lengthening pedicel, develops among the perianth segments. These gradually turn dry and yellow or brown, but scarcely shrivel or lose their shape. Fully mature, the fruit is ovoid, crowned by the shrivelled stigma, 5–10 mm. long, and conspicuously white. It is fleshy but utterly tasteless. Nothing is known of dissemination. The fruit seems not to attract animals; it dries up and turns black *in situ*. The abundant seeds (pl. V, fig. 3) are approximately 0.35 mm. long. They are ellipsoid in shape and of a shining chestnut-brown color, like minute footballs; the surface shallowly pitted by the collapse of external cell walls; the micropylar end somewhat contracted and darkened, the chalazal end obtuse, not tailed.

TISSUES; VASCULAR ANATOMY OF THE RECEPTACLE

On all external surfaces of the shoot, excepting those of the anthers, the stigma, and the inside of the pistil, there is an epidermis with a cuticle which is minutely striate. The ground tissue shows no particular peculiarities except the presence of many cells containing some substance (tannin ?) which stains deeply red with safranin and deeply black with osmic acid. The same

substance, apparently, is abundant in the cells of the epidermis of the anthers (the exothecium) and in the outermost cell layer of the ovules. The stigma is seen in sections of buds to be covered by an epidermis of columnar cells; as the flower matures, they become needle-shaped and separate from one another. They are evidently glandular and secrete a viscid material in which pollen grains catch.

Before describing the vascular system of the flower, one must say something of the anatomy of the stem. There is a thin vascular cylinder, with but few lignified cells, between the cortex and the large pith. The "nodes are unilacunar"; in the peduncle there are leaf traces from each gap, but no axillary bud traces; in the rachis, a flower trace of two bundles arises from the sides of each gap above the bract trace.

In all of the matters just mentioned, *Pleuricospora* agrees with *Newberrya* and *Pityopus* as I have already (5, 6) described them. A conspicuous difference is the complete absence of epidermal hairs in *Pleuricospora*.

The two bundles of the flower trace come together to form a vascular cylinder in the pedicel. In the receptacle, several whorls of bundles depart from this cylinder, not without considerable irregularity (pl. V, fig. 5). The typical picture is as follows: (a) First a whorl of four bundles passes out to the sepals. (b) Then, alternating with the sepal bundles, a whorl of four passes out to the petals. (c, d) Next, two whorls, each of four bundles, pass out to the stamens; the bundles to the stamens opposite the petals are immediately above the ones to the petals; the bundles to the stamens opposite the sepals are commonly a little higher. This lowering of the petalad stamen bundles is found also in *Pityopus*, where it is associated with the pairing of the nectaries opposite the petals; but there is no pairing of the nectaries in *Pleuricospora*. (e) A whorl of four carpel-dorsal bundles, placed above the petalad stamen bundles, ascends the walls of the ovary. (f) Finally, a whorl of four placental bundles ascends into the placentae. These use up the last of the vascular tissue.

Gaps may be either present or absent in the vascular cylinder above any particular bundle, or elsewhere; they are most usually present above the sepal and sepalad stamen bundles, most usually absent above the petal bundles. No carpel-lateral bundles, which would ascend the wall of the ovary in positions alternate with the carpel-dorsals, were mentioned above; but occasionally a more or less complete whorl of them may be found. Sometimes more than one bundle runs up the back of a single carpel. The supply to a placenta consists often of more bundles than one. My figure is based on several sets of serial sections; it represents the ideal receptacular vascular system as I understand it, rather than the actual structure of one individual.

DEVELOPMENT OF STAMENS AND POLLEN

I failed to follow the development of internal structure in the stamen from August till June. In early June, the cells of wall and tapetum and the microspore mother-cells are already distinct (pl. II, fig. 1). The wall consists of two or three layers of thin-walled cells, those of the outermost layer (the exothecium, containing much material stainable with safranin) being very much the largest.

All tapeta are short-lived; but they live long enough, in various flowering plants, to show differences in behavior. Cooper (4) has studied the occurrence of nuclear divisions in tapetal cells of many species, and finds three types of behavior: either the tapetal nuclei remain undivided; or they divide once, and the cells remain binucleate; or they divide an indefinite number of times, and the cells become multinucleate. No Ericales were among the plants he studied. The present species, if my eyes have not deceived me, conforms to none of Cooper's three types. By the time the pollen mother nuclei are in synapsis, the tapetum has already begun to degenerate, but still mitotic figures may be seen in it; mitosis seems always to be followed by cell division, and the tapetum comes to consist of uninucleate cells of varied sizes. The tapetum shrivels away to nothing without becoming an amoeboid mass; it is of the "Sekretionstapetum" type of Schnarf (13).

The development of pollen mother-cells into pollen grains takes place, in the climate of Sacramento, during a period of a week or two, while the anthers are about 2-3.5 mm. long.

As the anther enlarges and the tapetum degenerates, the pollen mother-cells enlarge, and walls, gradually increasing in thickness, appear about them. They round up. The stages of synapsis, diakinesis, heterotypic metaphase and anaphase, and the phases of homeotypic division were observed in succession (pl. II, figs. 4-8). In the heterotypic anaphase it was possible to count the chromosomes; the haploid number is twenty-six (pl. V, fig. 4). It was not perfectly easy to be certain of the count. I became convinced that twenty-six is the correct haploid number when I was able to see both anaphase groups in a single cell, from a direction between equatorial and polar, and to find the chromosomes corresponding in position, individual by individual, in the two groups. They seem to be all alike, ovoid in shape, and show a tendency to arrange themselves in definite rows.

When reduction division is complete, the wall of the pollen mother-cell having developed considerable thickness, cell division follows by simultaneous furrowing (pl. II, figs. 7, 8); and soon afterward one finds separate pollen grains (pl. II, fig. 9). Exactly this process has been described in very many flowering plants. It raises a number of questions, to which the answers are probably known although I have not located them. The wall

which develops about the pollen mother-cell, the wall which forms in the furrows between the pollen grains as fast as they cut in, and the walls about the separate grains, all seem to be of the same material: at least, they are all alike resistant to staining. What material is this? Does the wall of the pollen mother-cell become divided among the pollen grains, or does it dissolve, while each pollen grain forms its own wall?

I have not seen such a stage as Oliver (10) figures for *Sarcodes*, in which the original nucleus of the pollen grain has divided and a generative cell has formed against the wall of the pollen grain. It is quite possible that the generative cell originates in this fashion; I have seen it only in later stages, as a fusiform body of deeply staining cytoplasm lying free within the pollen grain and containing a nucleus which stains more deeply than the tube nucleus (pl. II, fig. 9). The mature pollen grain, mounted in liquid, is essentially spherical. The wall is marked by four lengthwise grooves (rarely five). Mounted in air, pollen grains become approximately cubical, as the four grooves on the sides and also the two ends are drawn in.

As was mentioned above, the final maturing of the pollen grains goes along with the elongation of the filaments, and is followed by the opening of the flowers and the dehiscence of the anthers.

Newly ripe pollen grains were tested for germination in hanging drops of tap water and of solutions of sucrose of concentrations from one to 30 per cent. There was no germination in tap water. Germination took place in every sugar solution tested; it was recognizable within five hours by the appearance of a little bump on one of the grooves of each pollen grain. It seemed most normal and abundant, and the growth of the pollen tube seemed most rapid, in the 20 per cent solution; here tubes 0.5 mm. long were seen after thirty hours. The more dilute solutions seemed hypotonic with respect to the contents of the pollen grains; they did not cause the grains to swell and burst, but caused the ends of the pollen tubes, where the walls must be weakest, to become swollen, sometimes to diameters as great as the pollen grains from which they had sprung. The more concentrated solutions caused no obvious damage but seemed to decrease the percentage of germination and to retard growth. The generative cell was seen to enter the pollen tube before its nucleus had divided (pl. II, fig. 10). Either the tube nucleus or the generative cell may enter the tube first.

Of the growth of the pollen tube under natural conditions, I know little. The pollen grains are caught on the stigma by some viscid substance secreted by the epidermal layer of needle-shaped cells. The pollen tubes grow along the cracks between the lobes of the stigma and down the style channel. In the ovary I have only occasionally been able to recognize pollen tubes, and I have not been able to see one growing from outside

into an ovule. The plugs closing old pollen tubes, mentioned by Oliver as occurring in *Sarcodes*, were recognized.

DEVELOPMENT OF OVULE AND SEED

Ovules are recognizable, up to about the time of reduction division in the anthers, as abundant hemispherical bumps on the placentae. I have missed seeing a series of stages including the differentiation of the archesporial cell, the "bending over" by which the ovule becomes anatropous, and the origin of the integument. As the pollen grains are ripening, one finds the archesporial cell (which, as is usual in Sympetalae, is itself the megaspore mother-cell) in synapsis or diakinesis (pl. III, fig. 1); the integument, of two layers of cells, is closing over the nucellus, which is a single layer of cells. Subsequently one finds a T-shaped megaspore tetrad (pl. III, fig. 2), of three minute cells and one large one in the chalazal position. In the latter, 2-, 4-, and 8-nucleate stages have been observed, and finally the mature embryo sac, consisting of an egg, two synergids, an endosperm mother-cell containing two polar nuclei, and three antipodal cells (pl. III, fig. 4). While the embryo sac develops, the three non-functional megaspores are absorbed, and so is the whole of the nucellus. There may be some increase in the number of cell layers of the integument; but the integument remains quite thin, and no jacket layer of columnar cells is formed about the embryo sac.

It has not been possible to follow the details of fertilization. It is clear that the pollen tube enters through the micropyle and creates a certain amount of wreckage in the micropylar end of the embryo sac. The egg remains clearly recognizable. In a single section I was able clearly to see one spherical sperm nucleus uniting with the egg nucleus, while another was uniting with the two polar nuclei (pl. III, fig. 5). These observations are in harmony, as far as they go, with those of Shibata (14) on *Monotropa uniflora*, in which he found the sperm nuclei, elongate when first discharged from the pollen tube, to become spherical as they reach respectively the egg nucleus and the polar nuclei, and only then readily stainable. Shibata (15) has mentioned the handsome strands of cytoplasm, extending from the original fusion nucleus in the endosperm, which he observed in living material of *Monotropa*. They are equally evident in microtome sections of *Pleuricospora* (pl. III, fig. 6).

The endosperm develops in the manner usual in Ericales. Before the zygote undergoes any divisions, the endosperm nucleus divides twice; each nuclear division is followed by a cell division, the walls falling at right angles to the axis of the embryo sac, so that a row of four cells is formed (pl. IV, figs. 1, 2). The zygote grows into the shape of a narrow tube, whose summit, in which lies the nucleus, penetrates into the second cell of the endosperm. Of the cells of the four-celled endosperm,

some or all may divide by further transverse walls; the second cell (the one surrounding the summit of the embryo) and the fourth (the one at the chalazal end) almost always do this; the first and third more frequently remain undivided. By these divisions the endosperm is converted into a row of six to eight cells. Longitudinal divisions also take place, converting the cells of the row into tiers of cells. The standard number of cells in the tier seems to be four, but this number is not at all constant; thus one may find a tier of four between the developing embryo and the micropylar end of the endosperm; six or eight in a section cut through the embryo; four in sections cut farther back; and only one at the chalazal end.

The first division of the zygote separates, by a transverse wall, a cylindrical cell toward the micropyle from a nearly spherical one toward the chalaza (pl. IV, fig. 3). The protoplasm in the cylindrical cell is gathered at the end which is against the spherical cell, and in later stages it is found to have secreted a wall cutting off a brief suspensor devoid of contents from a conical cell which has been designated as the hypophysis. The spherical terminal cell divides by two vertical walls into a cluster of four. Possibly division sometimes goes farther than this, but I have not been able certainly to recognize it. As the seed approaches maturity, stainable material accumulates in the living cells of the endosperm and embryo. It is evidently the same material in both structures; they are distinguishable only by position, not by staining reactions (pl. IV, fig. 4).

At the time of fertilization the embryo sac is surrounded by an integument partly of two layers of cells, but of three or more against some parts of the sides of the embryo and of several layers at the ends. Even before fertilization the outermost layer, except for a broad gap at the micropylar end, becomes markedly different from the others by an accumulation of tannin (?) as a hollow vesicle within each cell. During development after fertilization, the inner cells against the sides of the endosperm become flattened and finally almost—not quite completely—disappear. A certain number of thin-walled inner cells at the ends remain intact into the ripe seed. A group of antipodal cells can be detected in the chalazal end for some time. The outermost layer of cells becomes very thick-walled, especially on their lateral and inner surfaces; the tannin (if tannin it be) by which these cells are distinguished in earlier stages is perhaps a plastic material from which these thick walls are built. No terminal haustoria are formed on the endosperm, and no tails are formed on the seed by the collapse of functionless inner cells.

DISCUSSION

The most important contributions on the microscopy of the reproductive structures of Ericales have been those of Koch (9) on *Hypopitys*; Oliver (10) on *Sarcodes*; Stevens (17) on *Epigaea*; and Samuelsson (11) and Hagerup (8) on a variety of genera,

chiefly Scandinavian. These contributions have been duly summarized by Schnarf (13). *Pleuricospora* conforms to the characters of the order in a whole range of characters, among which may be mentioned the following: (a) flowers formed the year before they are to open; (b) the absence of an endothecium in the anthers; (c) the non-amoeboid tapetum in the anthers; (d) reduction division occurring in the anthers sooner than in the ovules; (e) "simultaneous" division of the pollen mother-cells; (f) pollen grains with two nuclei; (g) the channeled style; (h) ovules with a single integument and a thin nucellus which is soon absorbed; (i) embryo sac developed in "normal" fashion; (j) a young endosperm of four cells in a row; (k) the inner cell-layers of the integument absorbed, for the most part, by the endosperm.

The tapetum in which the cells continue to divide for some time and do not become multinucleate may be an ordinal character; I know of no data on this point from other Ericales.

The pollen grains which are solitary, not in tetrads, are not typical of the order; but they are altogether typical of the monotropoid alliance.

I know of no previous count of the chromosomes in any plant of the monotropoid alliance. Hagerup counted the chromosomes in many other Ericales and concluded that the fundamental number is six; the twenty-six chromosomes of *Pleuricospora* may be a set of $4n + 2$. This number is not in good harmony with the chromosome number of *Pyrola* ($n = 23$); it harmonizes well with the numbers in *Rhododendron* (a genus in which Sax (12) has found the chromosome number remarkably constant) and *Ledum* ($n = 13$) and in the Arbutae ($n = 13$ or 26).

In Ericaceae the integument is usually of several layers of cells at the time of fertilization; and the endosperm usually comes to consist of many cells. Most of the Pyrolaceae of Engler and Prantl (that is, the allies of *Pyrola* and of *Monotropa*) have a very thin integument; and in *Hypopitys* and *Pleuricospora* the endosperm is of very few cells. The nature of the endosperm in other Pyrolaceae, excepting *Sarcodes*, is not definitely known. In bulk both of integument and of endosperm, *Sarcodes* lies between the other Pyrolaceae and the Ericaceae.

The course of formation of the endosperm in *Hypopitys* and *Pleuricospora* shows striking identities, notably in the transverse divisions which take place in the second and fourth cells of the four-celled endosperm; but *Pleuricospora* differs from *Hypopitys*—and, indeed, from almost all other known Ericales—in the fact that the terminal cells of the developing endosperm do not take on a different appearance from the rest, and do not eventually collapse. Some of the details of the embryology of *Sarcodes* as figured by Oliver are different from corresponding stages of *Pleuricospora* and *Hypopitys*; Oliver has represented an embryo developing in the micropylar chamber of the four-celled endosperm, and a suspensor of two or three short, nucleated cells.

Hypopitys and *Monotropa* are closely related to a series of genera with parietal placentation, *Newberrya*, *Pityopus*, and *Monotropastrum* (Andres, 1, 2). *Pleuricospora* stands outside this circle, distinguished by a combination of characters of no great weight, but which nevertheless make it seem distinct: its completely glabrous character, the pattern of the anthers, its drying brown rather than black, its carpels almost constantly four rather than varying about eight as an average. I do not think that it is related to *Hypopitys* and its closest allies either as ancestor or descendant, but that it is a reasonably close collateral relative.

The direction of evolution by which these plants are related to the Ericaceae remains open for discussion. It is possible to conceive that *Pleuricospora*, with its simple endosperm and anthers opening through slits, is primitive; and that *Hypopitys* and its allies represent a line of evolution leading through *Sarcodes* and *Pterospora* to the Ericaceae, among which some of the Arbutoidae might be the nearest. I am much more inclined to read the series in the opposite direction, and to regard *Pleuricospora* as an end product of a line of evolution in which many of the specialized structures of the Ericaceae have been lost or reduced to their minimum essentials.

Sacramento Junior College,
Sacramento, California,
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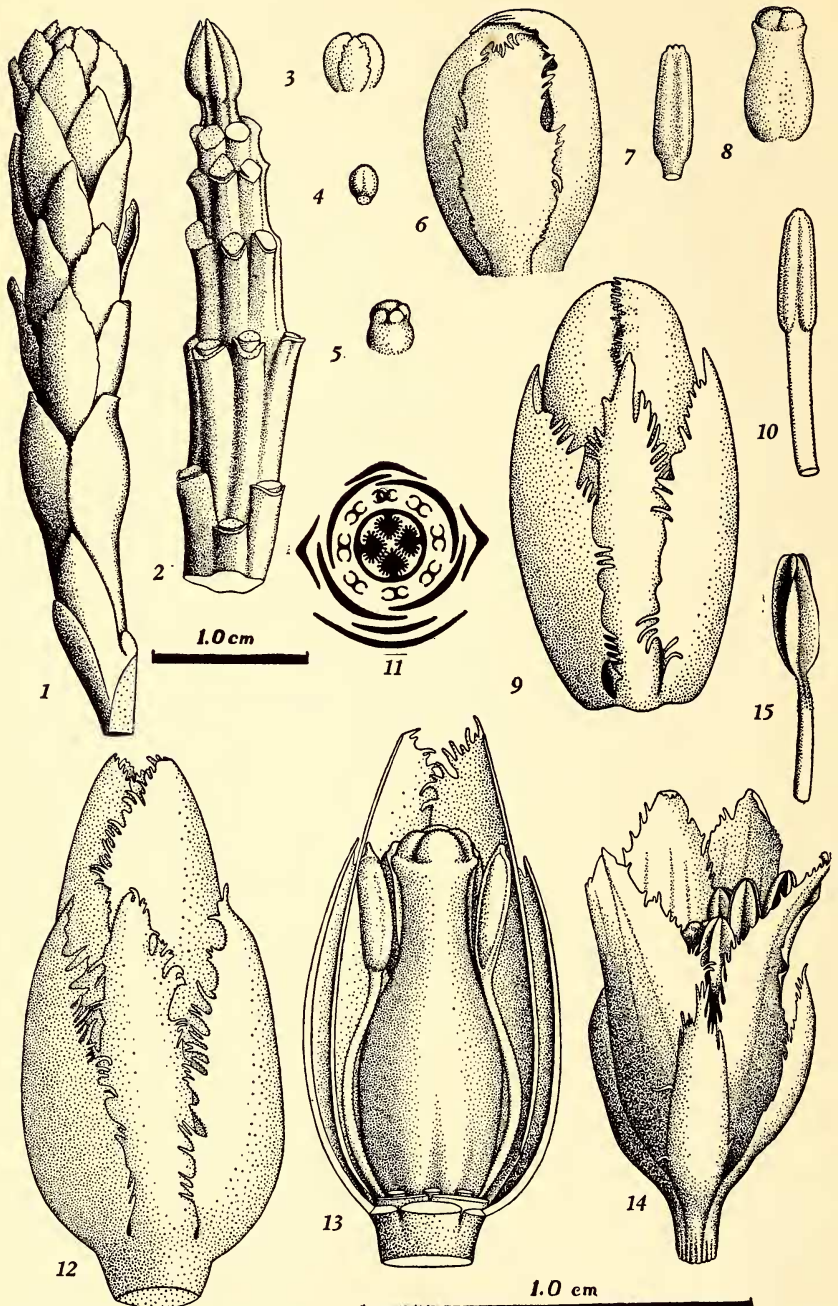


PLATE I. *PLEURICOSPORA FIMBRIOLATA* GRAY. Fig. 1. Young shoot, with leaves in whorls of four, $\times 2$. Fig. 2. Rachis of inflorescence, showing attachment of bracts and flowers in whorls of five, $\times 2$. Figs. 3, 4, 5. Young bud, stamen, and pistil $\times 5$. Figs. 6, 7, 8. Older bud, stamen, and pistil. Figs. 9, 10. Bud ready to open and stamen $\times 5$. Fig. 11. Floral diagram. Figs. 12, 13. Open flower and longitudinal section $\times 5$. Figs. 14, 15. Flower past anthesis and stamen $\times 5$.

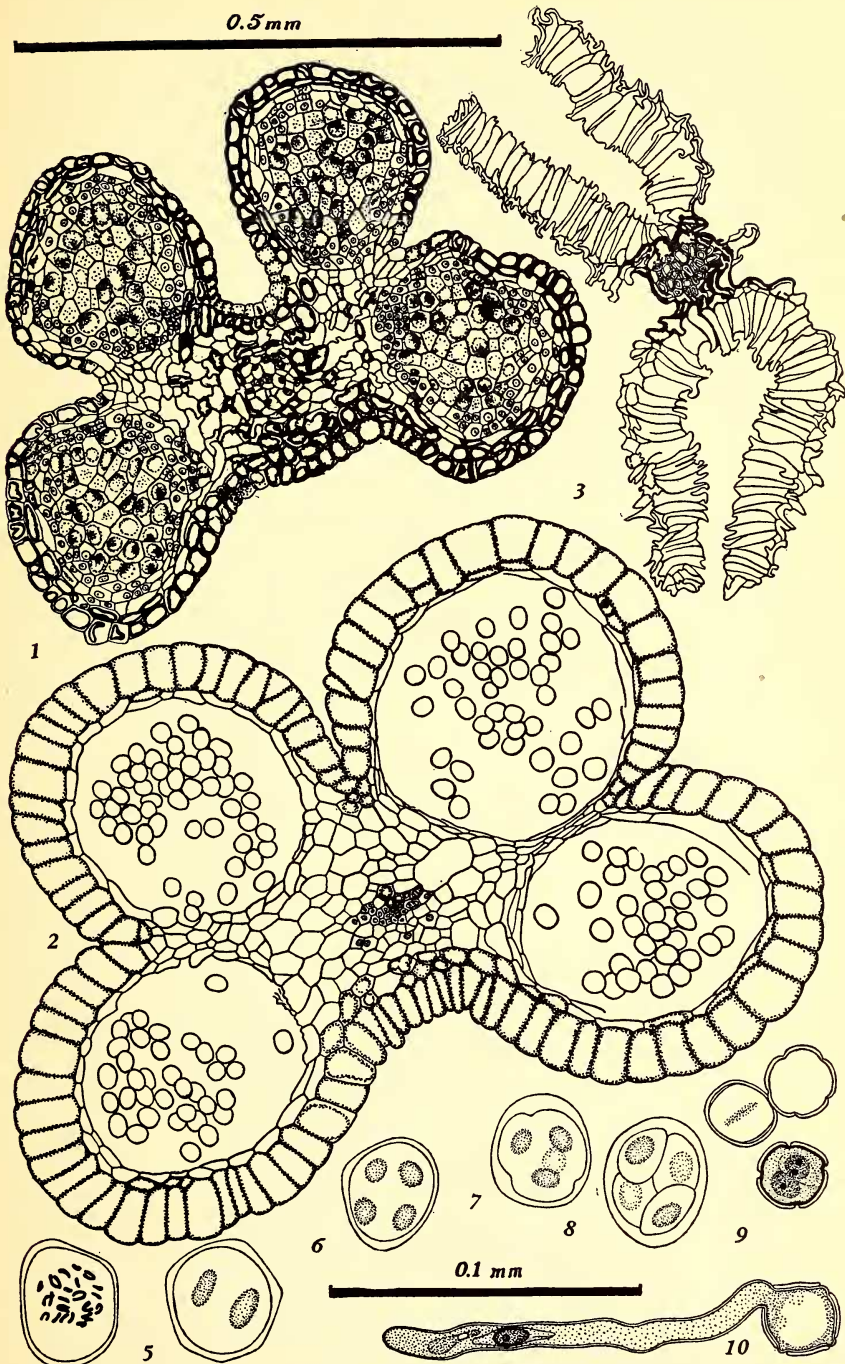


PLATE II. *PLEURICOSPORA FIMBRIOLATA* GRAY. Figs. 1, 2, 3. Cross sections of anther in successive stages $\times 125$. Figs. 4-9. Development of pollen grain $\times 400$. Fig. 10. Germinated pollen grain with pollen tube attached $\times 400$.

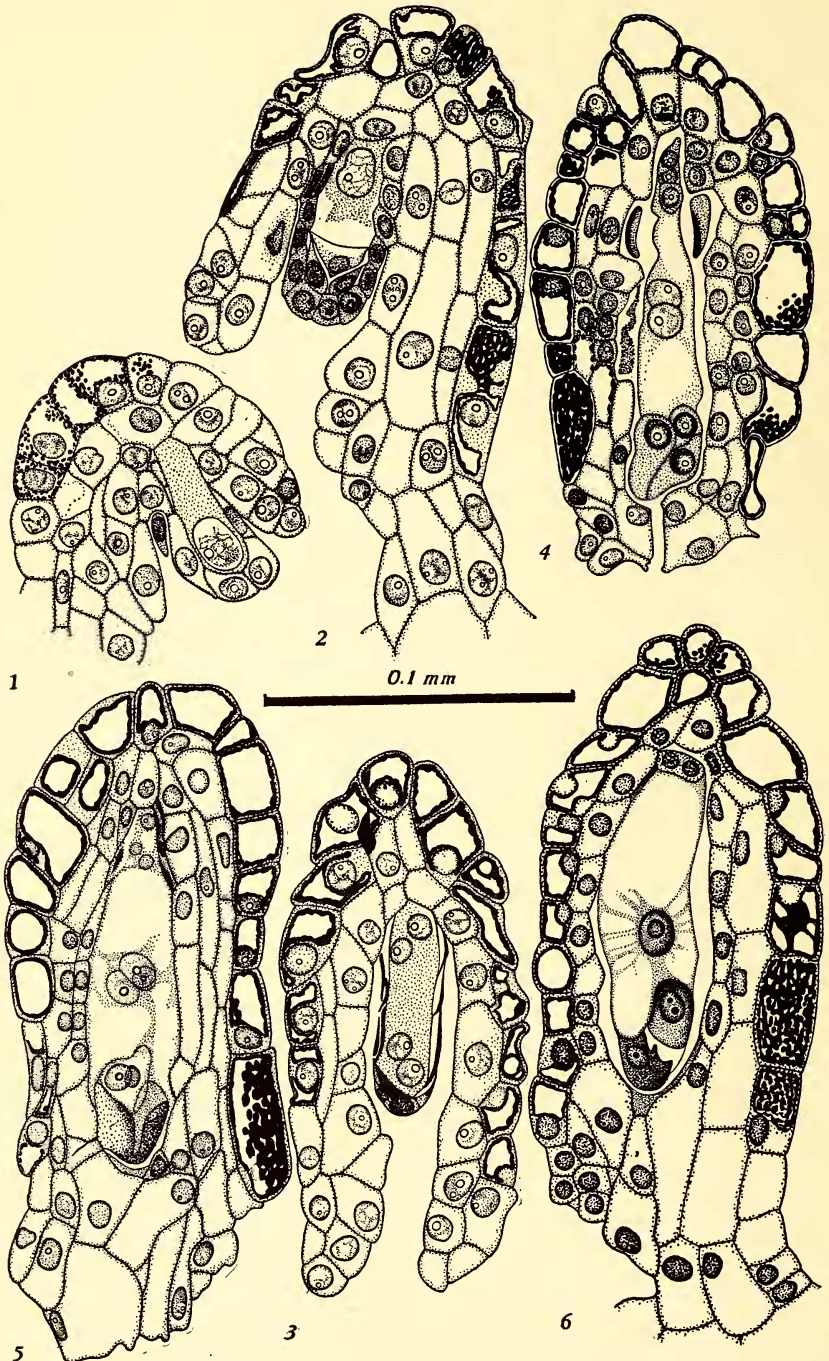


PLATE III. *PLEURICOSPORA FIMBRIOLATA* GRAY. Development of ovule. Fig. 1. Megaspore mother cell. Fig. 2. Megaspore tetrad. Fig. 3. Four-nucleate embryo sac. Fig. 4. Mature embryo sac. Fig. 5. Fertilization. Fig. 6. One-celled endosperm. All $\times 400$.

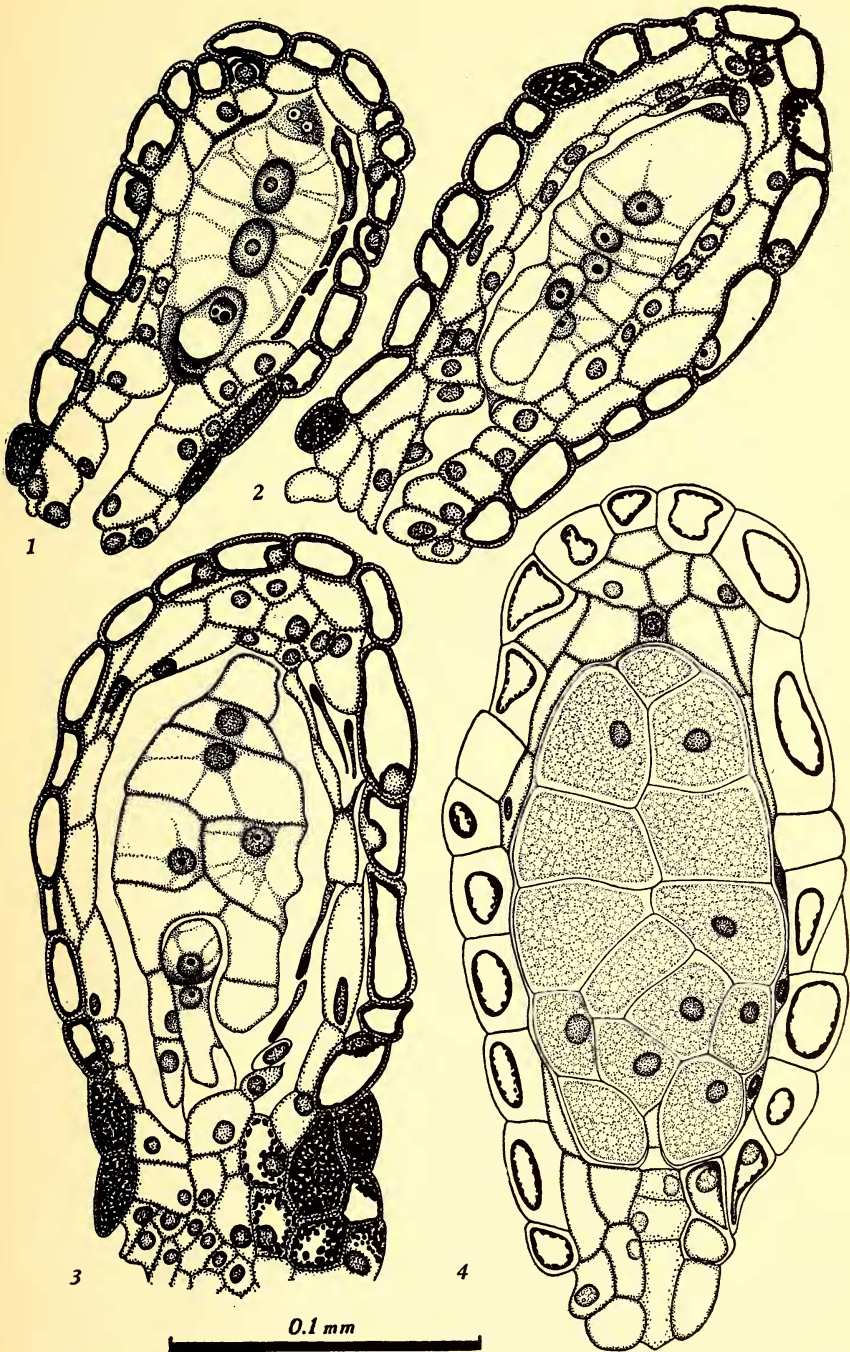


PLATE IV. *PLEURICOSPORA FIMBRIOLATA* GRAY. Development of seed. Fig. 1. Two-celled endosperm. Fig. 2. Four-celled endosperm. Fig. 3. Two-celled embryo. Fig. 4. Nearly ripe seed. All $\times 400$.

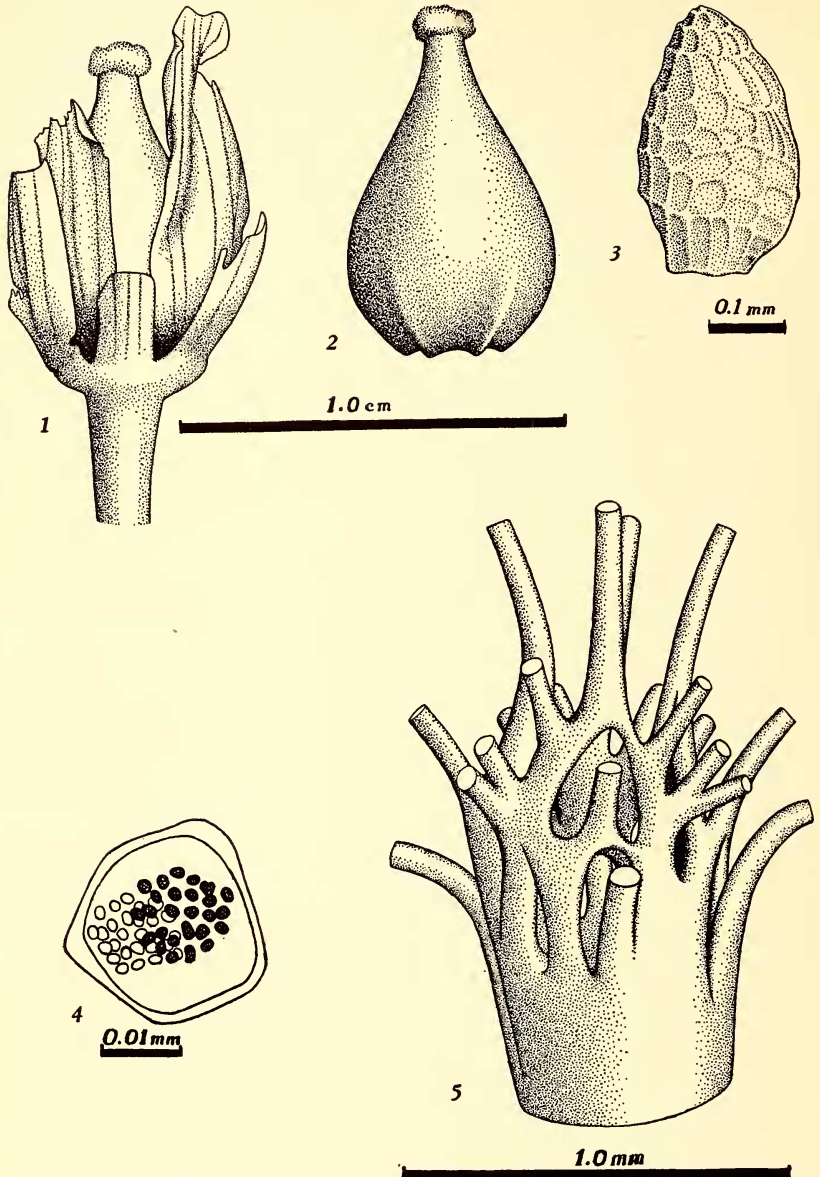


PLATE V. *PLEURICOSPORA FIMBRIOLATA* GRAY. Figs. 1, 2. Fruits $\times 5$. Fig. 3. Seed $\times 100$. Fig. 4. Heterotypic anaphase in pollen mother cell $\times 840$. Fig. 5. Reconstruction of the vascular system in the receptacle $\times 50$.